

Test for age-specificity in survival of the common tern

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ABSTRACT

*Much effort in life-history theory has been addressed to the dependence of life-history traits on age, especially the phenomenon of senescence and its evolution. Although senescent declines in survival are well documented in humans and in domestic and laboratory animals, evidence for their occurrence and importance in wild animal species remains limited and equivocal. Several recent papers have suggested that methodological issues may contribute to this problem, and have encouraged investigators to improve sampling designs and to analyse their data using recently developed approaches to modelling of capture-mark-recapture data. Here we report on a three-year, two-site, mark-recapture study of known-aged common terns (*Sterna hirundo*) in the north-eastern USA. The study was nested within a long-term ecological study in which large numbers of chicks had been banded in each year for > 25 years. We used a range of models to test the hypothesis of an influence of age on survival probability. We also tested for a possible influence of sex on survival. The cross-sectional design of the study (one year's parameter estimates) avoided the possible confounding of effects of age and time. The study was conducted at a time when one of the study sites was being colonized and numbers were increasing rapidly. We detected two-way movements between the sites and estimated movement probabilities in the year for which they could be modelled. We also obtained limited data on emigration from our study area to more distant sites. We found no evidence that survival depended on either sex or age, except that survival was lower among the youngest birds (ages 2-3 years). Despite the large number of birds included in the study (1599 known-aged birds, 2367 total), confidence limits on estimates of survival probability were wide, especially for the oldest age-classes, so that a slight decline in survival late in life could not have been detected. In addition, the cross-sectional design of this study meant that a decline in survival probability within individuals (actuarial senescence) could have been masked*

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by heterogeneity in survival probability among individuals (mortality selection). This emphasizes the need for the development of modelling tools permitting separation of these two phenomena, valid under field conditions in which the recapture probabilities are less than one.

1 Introduction

1.1 Measuring age-specific survival

Much effort in life-history theory has been addressed to the dependence of life-history traits on age, especially the phenomenon of senescence and its evolution (Mertz, 1975; Finch, 1990; Charlesworth, 1994; Ricklefs, 1998, 2000; Service, 2000; Partridge, 2001). Studies of long-lived iteroparous species have revealed two characteristic patterns, an increase in survival among younger age-classes (e.g. Bradley *et al.*, 1989; Charlesworth, 1994; Pugsek *et al.*, 1995) and a decrease among older individuals following a plateau in middle-age (Bradley *et al.*, 1989; Pugsek *et al.*, 1995; but see Loison *et al.*, 1999). The increase among younger individuals is usually explained by the positive influence of experience (e.g. gain of skills and knowledge of feeding areas), higher reproductive costs in inexperienced individuals (Viallefont *et al.*, 1995), and/or within-generation mortality selection (Curio, 1983; Endler, 1986; Forslund & Pärt, 1995). The decline among older individuals is usually interpreted as due to senescence (but see Blarer *et al.*, 1995).

Senescence is defined as 'age-related changes in an organism that adversely affect its vitality and functions, but most importantly, increase the mortality rate as a function of time' (Finch, 1990). Although senescent declines in survival have been well documented in humans and in domestic and laboratory animals, evidence for their occurrence and importance in wild animal species remains limited and equivocal (Nichols *et al.*, 1997; but see Pugsek *et al.*, 1995; Loison *et al.*, 1999).

Several difficulties in investigating age-related variation in survival in wild animal populations have led reviewers to treat evidence (and lack of evidence) of senescent decline with caution. Field studies estimate age-specific mortality rates by marking individuals within one or more cohorts and tracking the numbers of cohort members that survive through successive intervals. Because the number of survivors decreases with time (time and age are confounded at the cohort level), most field studies use multiple cohorts, followed for multiple years, in order to obtain reliable estimates of survival rates in older age-classes (e.g. Bradley *et al.*, 1989; Pugsek *et al.*, 1995; Nichols *et al.*, 1997). Several such studies have reported apparent age-specific decreases in survival rates in wild animal species (Gaillard *et al.*, 1994; Holmes & Austad, 1995a,b), especially long-lived seabirds (Rattiste & Lilleleht, 1987; Bradley *et al.*, 1989; Aebischer & Coulson, 1990; Dann & Cullen, 1990; Weimerskirch, 1992; Harris *et al.*, 1994; Pugsek *et al.*, 1995; Sagar *et al.*, 2000). However, several of these studies did not use mark-recapture methodologies that explicitly take into account recapture or resighting probabilities.

Observed patterns of age-related variation in survival may reflect any or all of four distinct phenomena.

- (1) Changes within individuals. The probability of death may decline with age within younger individuals as a result of increasing experience or decreasing reproductive costs (Charlesworth, 1994; Viallefont *et al.*, 1995), and may increase with age among older individuals as a result of actuarial senescence (McDonald *et al.*, 1996).

- (2) Secular changes in the environment. In studies following one or a few cohorts, all the individuals reach older ages within a specific set of years, usually the later years in the study. If survival is lower (or higher) for all individuals in these years because of changes in the environment, this can lead to a spurious appearance of lower (or higher) survival among older birds, unless year effects are controlled for (e.g. Aebischer & Coulson, 1990).
- (3) Age-specific emigration. If the probability that an individual leaves the study-area decreases (or increases) with age, this can lead to a spurious increase (or decrease) in apparent survival with age (discussed in Loison *et al.*, 1999).
- (4) Mortality selection (phenotypic selection; Endler, 1986). If different individuals have constitutionally higher or lower probability of death throughout their lives ('mortality risk' in human demography), the proportion of individuals with lower mortality risk will increase in the older age-classes through selective survival (Vaupel & Yashin, 1985a; Service, 2000), whether or not survival changes with age within individuals.

Although it is theoretically possible to disentangle the four phenomena listed above by careful study design and data analysis, this has never been done in studies of wild animals. Most published studies have been based on data from a single study-site, assuming that emigration is either negligible or independent of age. A few studies of senescence have considered variability among years (Harris *et al.*, 1994; Rattiste & Lilleleht, 1995; Nichols *et al.*, 1997; Loison *et al.*, 1999), but large sample sizes are required to separate effects of age and year, so the statistical power of such studies is often low, especially for the oldest age-classes (Nichols *et al.*, 1997). The main obstacle to considering within-generation mortality selection is methodological. Statistical inference methods accounting for heterogeneity in mortality risks among individuals have been developed and used successfully in populations of humans or captive animals (e.g. Vaupel & Yashin 1985a,b; Service, 2000). However, the modelling tools required to use such approaches are not yet available in situations where the probability of observing/capturing individuals is less than one (Lebreton, 1995), which is typical in field studies of wild animals (Lebreton *et al.*, 1992; Nichols, 1992; Clobert, 1995; Nichols & Kendall, 1995). Such tools have been developed for capture-recapture models using recovery data (Burnham & Rexstad, 1993; Pledger & Schwartz, this issue).

As emphasized by Nichols *et al.* (1997), inferences about senescence in studies that have not explicitly modelled resighting probability are not necessarily incorrect, but use of such approaches is an important criterion to assess the reliability of inferences. In addition, recent advances in capture-recapture modelling tools offer more flexibility and permit investigation of the influence of age on local survival (i.e. while accounting for dispersal within the study area: Brownie *et al.*, 1993; Clobert, 1995; Nichols & Kendall, 1995). The fact that only a few studies conducted in the wild have yielded strong evidence for senescent decline in survival (e.g. McDonald *et al.*, 1996; Loison *et al.*, 1999) calls for careful examination of possible methodological issues that might obscure the phenomenon of interest. Our objective in this paper is to contribute to the growing list of studies that have used robust approaches to testing hypotheses about senescence (e.g. Gaillard *et al.*, 1994; Nichols *et al.*, 1997).

1.2 Outline of this study

This study was designed to address the influence of age on survival in common terns (*Sterna hirundo*). It was nested within a long-term study in which large numbers of

common terns have been banded in the years of hatching (Nisbet *et al.*, 1984; forthcoming), so that marked individuals from 24 different age-classes were present in the local population at the outset of the study. We conducted a three-year capture-recapture study within this marked population, identifying a large sample of known-aged birds with an age-range of 2-25 years in the first year and recapturing surviving birds in the second and third years. We conducted the study at two sites, thereby measuring and controlling for age-specific dispersal between these sites; we also obtained limited information on emigration to other sites in the region. We tested for a possible influence of sex on survival, because evidence of such an effect has been found in several species of seabirds (Mills, 1989; Aebischer & Coulson, 1990; Weimerskirch, 1992). Because the study was cross-sectional (estimating survival and movement rates for one year only), it controlled for any influence of year-to-year variations in survival or dispersal rates. This advantage was offset, however, by limited sample sizes for the oldest age-classes, and by the absence of methods to test for possible effects of within-generation mortality selection.

2 Study-sites and field methods

2.1 Bird Island

The primary study-site was Bird Island, Massachusetts, USA (41°40'N, 70°43'W). Bird Island is a glacial till island in the upper part of Buzzards Bay, with area 0.5-0.6 ha and maximum elevation 2.4 m above mean high water. Common terns occupy 0.3-0.35 ha on the lower parts of the island, nesting on coarse sand, shells, cobbles, and tide wrack, with partial to complete vegetation cover of herbaceous plants and grasses (Nisbet *et al.*, 1984, 1990). Numbers of common terns increased from about 250 nesting pairs in 1968-70 to 500 pairs in 1978, 1000 pairs in 1985, and 1880 pairs in 1989, levelling off at 1780-2023 pairs during 1989-97 (Nisbet, 1973, 1978; Nisbet *et al.*, 1984; and unpublished data). During this study, counts of nests were 1828 in 1995, 1780 in 1996 and 2023 in 1997. All these counts refer to nests started during the peak period of laying between 7 May and 8 June; in most years since 1988, 200-300 additional nests were started after 8 June.

The average breeding success of common terns at Bird Island was about two fledged chicks per pair in 1970-86, but fell to about 1.2 fledged chicks per pair in 1988-97 (Nisbet, forthcoming). Since durable bands became available in 1975 (Nisbet & Hatch, 1988), we have banded about half of the chicks raised on the island in each year. Many birds banded before 1975 were subsequently trapped and rebanded with durable bands (Nisbet & Hatch, 1988). Common tern chicks have also been banded in large numbers at many other sites in the north-eastern USA and south-eastern Canada (Hays *et al.*, 1999). By 1995, about 40% of the breeders at Bird Island were banded and of known age, but this proportion fell to about 36% in 1997, probably because of poor recruitment of birds raised on the island after 1987 (Nisbet, unpublished data). By 1997, 7% of the birds trapped at Bird Island had been banded as chicks at other sites, ranging from Cedar Beach, NY (250 km WSW) to Sable Island, NS (950 km ENE); 3% had been banded as breeding adults at other sites. Adult common terns (of unknown ages) were also banded at Bird Island in most years, especially in 1975, 1983 and from 1986 onwards (Nisbet, 1978, 1996; Nisbet & Hatch, 1988; Nisbet *et al.*, 1984).

The capture-recapture study was conducted in 1995-1997. In each year, we marked the first 1620-1821 nests on the island, usually on the day the first egg

was laid. We attempted to catch a uniform sample of birds within each day's stratum of new nests, randomizing the sampling in space by progressing systematically around the island and trapping on all nests until the desired sample size had been achieved. We also trapped mates on nests selected for special studies (about 7% of all nests in 1995, 8% in 1996, and 5% in 1997). We attempted to sample the same proportion of birds (45%) within each stratum, but in fact slightly oversampled early- and undersampled late-nesting birds. We did not sample birds that laid after 4 June systematically in any year, although we trapped some late birds for special studies in each year. Most of the birds that laid after 4 June were either 2-4 years old or older birds relaying after earlier failures (Nisbet *et al.*, 1984). Hence, our design should have yielded representative samples of birds ≥ 5 year in each year, but would probably have undersampled birds aged 2-4 years.

2.2 Ram Island

Our second study-site was at Ram Island (41°37'N, 70°48'W), 10 km SW of Bird Island. Following a restoration project (Harlow, 1995), this site was reoccupied by common terns in 1992; numbers of nests increased (almost entirely by immigration) from 98 in 1993 to 325 in 1994, 815 in 1995 and 1323 in 1996, declining to 1183 in 1997 (total-season counts: Harlow, 1995; and unpublished data). This site was not included in our original study design, but was added during the 1995 season after we found that some birds had moved there from Bird Island. We, and others, trapped 377 breeding adults in 1995, 460 in 1996, and 801 in 1997 (23%, 18% and 34% of breeders, respectively). Trapping at Ram Island did not follow a stratified random sampling design, but was carried out throughout the colony site and throughout the breeding season, so it should have yielded a reasonably representative sample of birds present in each year. Unbanded birds trapped in 1995 were banded and are included in the study. Most banded birds encountered at Ram Island had been marked as chicks at Bird Island or Great Gull Island (see below), but some of these were 5-20 years old in 1995 (i.e. had probably bred elsewhere before moving to Ram Island) and many had been banded as breeders at Bird or Great Gull Islands. Because some breeders had moved from Bird Island to Ram Island, and a few moved back (see the Results section), we include data from both islands in some analyses, even though the sampling designs were somewhat different.

2.3 Other sites

We also use data from the two largest breeding colonies of common terns in the region, which together comprised $> 80\%$ of the common terns nesting within 150 km of Bird and Ram Islands. At Great Gull Island (41°12'N, 72°07'W: 130 km WSW of Bird Island), numbers of common terns increased from 8000 pairs in 1995 to 9500 pairs in 1997 (Sommers & Alfieri, 1998). Large but unspecified numbers of breeding adults at this site were trapped in each year (Hays *et al.*, 1999). At Plymouth Beach (41°58'N, 70°39'W: 45 km NNE of Bird Island), numbers increased from 3900 pairs in 1994 to 4957 pairs in 1997 (S. Hecker, personal communication). Adults were not trapped at this site in 1996 or 1997, but we trapped 1034 adults there in 1994 (13% of breeders), in part to search for birds that had been trapped at Bird Island in 1991-92 (Nisbet, 1996) and might have moved to Plymouth Beach in 1992-94.

2.4 Trapping and handling

Birds were trapped in treadle traps set over the eggs. At Bird Island, unbanded birds were released immediately; banded birds were weighed, measured, and palpated for the presence of an egg in the oviduct. At Ram Island, most unbanded birds were banded, but few birds were measured until 1997. To minimize errors, band numbers were read twice, before and after recording. Only 5 of 2113 band numbers recorded could not be matched to banding records. Three of these were traced to errors at the time of banding or data entry and were corrected; the other two could not be corrected. Although some other potential errors might have been missed, we believe that the overall error rate was $< 0.2\%$.

Among 1625 banded birds identified at Bird Island, 1421 (87%) could be sexed based on characters recorded in one or more years (including trappings in years prior to 1995 for many individuals). Altogether, 823 birds (51%) were trapped on incomplete clutches and were sexed by the presence or absence of a palpable egg in the oviduct and/or by body mass (Wendeln & Becker, 1996). A further 191 (12%) were sexed by these characters in their mates, and 407 (25%) by bill-length and/or head-length, either alone or in combination with those of their mates (Coulter, 1986; Nisbet, forthcoming). Birds were sexed by bill-length or head-length alone ($n = 142$) only if these characters were extreme (> 39.1 mm or 78.2 mm, respectively, for males; < 35.8 or 76.7 mm, respectively, for females). Because these characters were used conservatively, we believe that the overall misclassification rate was $< 1\%$. Only a few birds were sexed at Ram Island except in 1997.

2.5 Potential band losses

All birds included in this study were banded with incoloy bands, so the probability of band loss is very low or zero (Nisbet & Hatch, 1988). We cannot evaluate the likelihood of band removal by humans in the winter quarters (Becker & Wendeln, 1996), but we assume that any such removal is unlikely to be age-specific.

3 Statistical methods

3.1 Sample definition

The initial marked sample is defined as all birds banded at any location in or before 1995, known to have been ≥ 2 years old in 1995, and encountered in one or more years during 1995-97 at Bird and/or Ram Islands. The two recaptured samples consist of birds captured at Bird and/or Ram Islands in 1996 and 1997. Designating a year of capture as 1 (Bird Island) or 2 (Ram Island) and a year without capture as 0, a capture history during the three years (111, 110, 100, 222, 220, 200, etc) was compiled for each bird. For eight birds that were trapped on both islands in the same year, the site of first encounter was used in the capture history. The sample was divided into 24 cohorts of known age (2-25 years old in 1995), one cohort known to be ≥ 16 years old in 1995 (banded as early-breeding adults in or before 1984), and one cohort of unknown ages (banded as adults in or after 1985). For some analyses, sex was treated as an additional state variable. To avoid bias resulting from retrospective classification (Buckland, 1982), we used sex information only for birds that were (or could have been) definitively sexed in or before 1995.

3.2 Modelling procedures and model selection

The full data set included a large number of possible states (26 age-classes, 3 'sexes'), with several different parameters to be estimated for each combination of states; many of the cells (especially those reflecting movements between sites or those for very old birds) were empty. Throughout the analyses, we pooled birds aged 2 and 3 years in 1995, because few 2-year-old birds were trapped; this pooled age-class was treated as 3 years old in models with a parametric dependence of survival or recapture probability on age. Because sample sizes were too small to estimate parameters individually for age-classes between 16 and 25 years while considering the effect of sex, we initially pooled all birds ≥ 16 years old in 1995 (including birds banded as adults prior to 1984); this pooled age-class was treated as 16 years old in parametric models. This reduced the number of age-classes from 26 to 14 (Table 1). We then conducted the analysis in several sequential steps, starting with models including two covariates (age and sex). First, we analysed data for the primary site (Bird Island) only, using data only for birds of known sex (Table 1). We used this data set to estimate local survival (probability of surviving from year 1 to year 2 and returning to Bird Island in year 2) and to assess the influence of age and sex on local survival. Finding no influence of sex, we then pooled all three sexes (increasing sample size by incorporating birds of unknown sex) for the next step in analysis. For this step, we treated birds aged 16-19 years as separate age-classes, but we pooled all birds ≥ 20 years old in 1995 because of small sample sizes. This reduced the number of age-classes from 26 to 18.

TABLE 1. Data for known-age, known- and unknown-sex individuals (Bird Island only)^a

Capture history ^b	Age in 1995 (yr)														Sex
	3 ^c	4	5	6	7	8	9	10	11	12	13	14	15	16 ^d	
111	0	2	1	5	1	4	9	2	3	2	1	2	1	5	M
110	2	2	1	0	4	18	4	9	7	6	0	1	3	3	M
101	2	0	0	3	3	12	5	5	4	2	1	3	0	4	M
100	5	1	2	5	15	24	16	10	9	10	3	4	2	6	M
011	4	0	2	2	5	2	2	2	2	4	0	2	1	3	M
010	12	2	1	2	4	9	6	2	5	4	0	1	1	3	M
001	28	3	2	6	7	10	2	3	3	6	2	4	0	1	M
111	2	3	2	1	2	6	6	1	1	2	2	2	1	1	F
110	1	1	6	8	5	5	11	4	6	4	3	3	1	1	F
101	0	1	3	5	6	12	8	4	6	3	2	6	2	2	F
100	11	2	6	10	13	30	14	12	16	7	1	4	3	6	F
011	9	2	0	1	2	9	5	6	7	3	0	3	2	1	F
010	25	4	5	5	6	15	13	6	7	6	1	3	1	6	F
001	36	3	3	8	4	8	12	5	11	2	1	3	1	2	F
111	0	0	1	0	0	2	1	0	0	0	0	0	0	1	U
110	1	0	0	1	2	1	2	0	0	0	0	0	1	0	U
101	0	0	3	3	0	3	0	0	0	1	0	0	0	1	U
100	3	0	0	3	8	12	4	0	0	1	2	4	4	2	U
011	0	0	0	1	3	2	2	0	0	0	0	1	0	0	U
010	12	3	1	2	4	5	0	1	2	0	0	1	0	0	U
001	14	2	2	2	5	7	3	3	3	2	2	0	2	1	U

^a A complete data set, with capture histories of all birds included in this study ($n = 2367$), has been posted on the EURING databank website (<http://www.nioo.knaw.nl/EURING.HTM>).

^b History in 1995, 1996, 1997: 1, trapped at Bird Island; 0, not trapped at Bird Island.

^c Includes all birds aged 2 or 3 yr.

^d Includes all birds aged ≥ 16 yr (range, 16-25).

The survival probability estimated using data from only one site reflects both true survival and permanent emigration away from that site (Brownie *et al.*, 1993; Nichols & Kendall, 1995); the corresponding estimate is likely to underestimate true survival. If data from other locations are available, it is possible to account for emigration to other study sites and to obtain estimates of survival corrected for movement among sites, using multistate models (Brownie *et al.*, 1993; Nichols & Kendall, 1995; Spendelow *et al.*, 1995). We next analysed data from both sites, estimating two-site survival (probability of surviving from year 1 to year 2 and returning to either site in either year 2 or year 3) and movement rates (conditional probability that a bird trapped at one site in year 1 and surviving to year 2 moved to the other site in year 2). For all two-site models, we further pooled age-classes into four groups, because sample sizes were too small to estimate all parameters for 18 cohorts. We selected these groups based on prior knowledge of the species (Nisbet *et al.*, 1984; Galbraith *et al.*, 1999), while ensuring that each was large enough to estimate most parameters (Table 2). Group 1 (2-4 years old in 1995) represented inexperienced breeders, Group 2 (5-9 years) represented young adults, Group 3 (10-14 years) represented mature adults, and Group 4 (≥ 15 years) represented the oldest breeders. We were unable to separate 4-year-old birds from younger birds, or 15-year-old birds from older birds, as in the earlier analysis, because of small sample sizes. We hypothesized that survival might be lower in Group 1 and/or Group 4 than in Groups 2 and 3. For some two-site models, we constrained movement rates to be the same for all of these grouped age-classes.

TABLE 2. Data from known and unknown-sex individuals (Bird and Ram Islands)

Capture history ^b	Age-class in 1995 ^a			
	1	2	3	4
222	0	2	1	1
220	1	7	1	1
210	1	0	0	0
202	5	10	4	0
201	1	1	0	0
200	28	35	10	5
122	0	2	0	0
121	0	0	1	0
120	0	3	0	1
112	0	2	0	0
111	7	41	19	10
110	7	66	43	11
102	0	7	7	1
101	3	66	37	10
100	22	150	78	31
022	9	6	6	0
021	0	0	2	1
020	74	25	9	5
012	1	3	3	1
011	15	38	32	7
010	56	75	35	18
002	142	52	15	7
001	86	80	48	9

^aAge-classes: 1 = [2-4 yr], 2 = [5-9 yr], 3 = [10-14 yr], 4 = [≥ 15 yr].

^bState notation: 1 = Bird Island; 2 = Ram Island; 0 = not encountered.

Finally, finding no evidence that age influenced survival or movement rates, we pooled all birds into one group (increasing sample size by incorporating birds of unknown age) to obtain a single set of estimates of survival and movement rates.

All data were analysed using program MARK (White & Burnham, 1999). Model selection was based on AICc, a modification of Akaike's Information Criterion incorporating a correction for small sample size (Anderson & Burnham, 1998). For one-site models, we used QAICc, incorporating a further correction for extradispatch (Burnham & Anderson, 1998). We used QAICc because there is no objective criterion to assess when the extradispatch parameter \hat{c} is sufficiently small to use AICc (e.g. Littel *et al.*, 1996, recommended using a lower value of \hat{c} than that recommended by Burnham & Anderson, 1998). We did not use model averaging to account for model uncertainty (Burnham & Anderson, 1998), because estimation of standard errors was not possible for all parameters in models with a large number of age-classes or states (i.e. 'estimated standard error' = 0).

3.2.1 Local survival probability at Bird Island. Individuals included in this analysis were recaptured at Bird Island in 1995, 1996 and/or 1997, were of known sex as of 1995 and of known age ($n = 826$, Table 1). For each cohort (ages 2-3, 4, 5...19 and ≥ 20) and each sex, recapture histories were modelled using four parameters: two time-specific survival probabilities: ϕ_{95} and p_{96} , and two time-specific recapture probabilities: p_{96} and p_{97} . ϕ_{96} and p_{97} cannot be estimated separately. Thus, for each cohort and each sex, only one survival and one recapture probability were estimated (ϕ_{95} and p_{96}), plus the product $\phi_{96} \times p_{97}$. We accounted for the influence of cohort on time-specific parameters (i.e. individual histories were modelled using time- and cohort-specific survival and recapture probabilities). That model can be denoted as: p_{t^*c}, ϕ_{t^*c} , where the subscript t denotes time and c denotes cohort. Each cohort reaches age a in year t , and no other cohort can reach the same age in the same year, that is, the combination of cohort and year corresponds to a unique age. Consequently, the model can also be denoted as: p_a, ϕ_a , where a denotes age. In the most general model, p and ϕ were not only dependent on age, but also on sex: p_{a^*s}, ϕ_{a^*s} , where s denotes sex. Sex was treated as a group effect. In that model there is one product $p_{96} \times \phi_{97}$ per cohort and sex whose components cannot be estimated separately. Note that we did not constrain these products. Consequently, for each model considered, the number of parameters reported as included in the model (Tables 3 and 4) includes products. This number depends on the number of 'groups' initially specified in the data matrix, not the number of 'cohorts' considered when specifying models.

3.2.2 Survival and movement probabilities between islands. As previous steps did not provide evidence of an influence of sex on survival or recapture probabilities, sex was not included in the next stage in modelling. The models we used were parameterized as follows (Brownie *et al.*, 1993): (1) p_a^r is the probability of capturing an individual of age a in stratum (site) r , given that the individual is alive and present in the study-area. (2) S_a^r is the probability that an individual in stratum r survives from age a to age $a + 1$. (3) ψ_a^{rs} is the probability that an individual in stratum r at age a is in stratum s at age $a + 1$, given that it survived to age $a + 1$. Because of the large number of parameters required to model survival, recapture probability, and movement probability as functions of age and site, we grouped age-classes into four groups as described above (Table 2). Because only a few birds

TABLE 3. Influence of age and sex on survival and recapture probabilities (Bird Island only)

	Model ^a	QAICc	NP ^b
p	$\phi_{(2-3, \geq 4)}$	1673.90	33
p	ϕ	1676.03	33
p	$\phi_{((2-3, \geq 4)+s)}$	1677.94	34
p	$\phi_{((2-3, 4, \geq 5)+s)}$	1678.61	35
p	$\phi_{((2-3, 4, 5, \geq 6)+s)}$	1679.00	36
p	$\phi_{(s)}$	1679.11	33
p	$\text{Logit}(\phi_a) = \alpha + \beta_1.a$	1679.15	33
p	$\phi_{((2-3, 4, \dots, \geq 8)+s)}$	1680.35	38
p	$\phi_{((2-3, 4, \dots, \geq 7)+s)}$	1680.90	37
p	$\text{Logit}(\phi_{a+s}) = \alpha + \beta_1.a + \beta_2.s$	1681.25	34
p	$\text{Logit}(\phi_{a+a^2+s}) = \alpha + \beta_1.a + \beta_2.a^2 + \beta_3.s$	1681.58	34
p	$\phi_{((2-3, 4, \dots, \geq 9)+s)}$	1682.35	39
p	$\phi_{(a^*s)}$	1683.26	35
p	$\phi_{((2-3, 4, \dots, \geq 10)+s)}$	1683.26	40
p	$\phi_{((2-3, 4, \dots, \geq 11)+s)}$	1684.87	41
p	$\phi_{((2-3, 4, \dots, \geq 12)+s)}$	1686.59	42
p	$\phi_{((2-3, 4, \dots, \geq 13)+s)}$	1688.79	43
p	$\phi_{((2-3, 4, \dots, \geq 14)+s)}$	1689.57	44
p	$\phi_{((2-3, 4, \dots, \geq 15)+s)}$	1689.79	45
p	$\phi_{(a+s)}$	1691.20	46
p	$\phi_{(a)}$	1693.19	43
p	$\phi_{(a^*s)}$	1702.97	59
$p_{(s)}$	$\phi_{(a^*s)}$	1704.52	60
$p_{(a+s)}$	$\phi_{(a^*s)}$	1721.72	71
$p_{(a)}$	$\phi_{(a^*s)}$	1733.50	73
$p_{(a^*s)}$	$\phi_{(a^*s)}$	1770.20	96

^aSee text for notation.^bNumber of parameters in model.

moved from Ram Island to Bird Island, our initial model included a movement probability in this direction that was independent of age.

4 Results

4.1 Local survival probability at Bird Island

The extradisersion parameter \hat{c} was equal to 0.96 (p_{a^*s} , ϕ_{a^*s} , Table 3, 1000 simulations). We first sought the lowest-QAICc model among simplifications of the general model for recapture probability. There was no evidence of an influence of age or sex on recapture probability (Table 3). We used the model with constant recapture probability (p , ϕ_{a^*s}) to continue model selection. A comparison between models including the effect of age as a factor (i.e. one survival probability per age-class; p , ϕ_{a^*s} ; p , ϕ_{a+s} ; p , ϕ_a) and models that did not include age (p , ϕ_s ; p , ϕ) yielded no evidence of an influence of age on survival. We did not find evidence of an influence of sex on survival either (Table 3).

In the next step, we used the lowest-QAICc model with age-specific survival probabilities (i.e. p , ϕ_{a+s} , Table 3) and progressively set survival parameters corresponding to consecutive age-classes equal, starting with the oldest individuals. This led to a model with two age-specific survival probabilities (p , $\phi_{((2-3, \geq 4)+s)}$). This model has only 2 survival probabilities: one for birds aged 2- or 3-years, and one

TABLE 4. Influence of age on survival and recapture probabilities; data from known and unknown-sex individuals (Bird Island only)

	Model	QAICc	NP
p	$\hat{\phi}_{(2-3, \geq 4)}$	1880.29	22
p	$\hat{\phi}_{(2-3, 4, 5, \geq 6)}$	1880.68	24
p	$\hat{\phi}_{(2-3, 4, \geq 5)}$	1880.83	23
p	$\hat{\phi}$	1881.30	21
p	$\hat{\phi}_{(2-3, 4, \dots, \geq 8)}$	1881.57	26
p	$\hat{\phi}_{(2-3, 4-18, \geq 19)}$	1881.57	23
p	$\hat{\phi}_{(2-3, 4-17, \geq 18)}$	1881.64	23
p	$\hat{\phi}_{(2-3, 4-19, \geq 20)}$	1881.69	23
p	$\hat{\phi}_{(2-3, 4-16, \geq 17)}$	1881.87	23
p	$\hat{\phi}_{(2-3, 4-15, \geq 16)}$	1882.02	23
p	$\hat{\phi}_{(2-3, 4, \dots, \geq 7)}$	1882.08	23
p	$\text{Logit}(\hat{\phi}_a) = \alpha + \beta_1 \cdot a$	1883.20	22
p	$\hat{\phi}_{(2-3, 4, \dots, \geq 9)}$	1883.24	27
p	$\hat{\phi}_{(2-3, 4, \dots, \geq 10)}$	1884.78	28
p	$\hat{\phi}_{(2-3, 4, \dots, \geq 11)}$	1886.76	29
p	$\text{Logit}(\hat{\phi}_{a+a^2}) = \alpha + \beta_1 \cdot a + \beta_2 \cdot a^2$	1887.22	23
p	$\hat{\phi}_{(2-3, 4, \dots, \geq 12)}$	1886.86	30
p	$\hat{\phi}_{(2-3, 4, \dots, \geq 13)}$	1890.79	31
p	$\hat{\phi}_{(2-3, 4, \dots, \geq 14)}$	1892.55	32
p	$\hat{\phi}_{(2-3, 4, \dots, \geq 15)}$	1894.66	33
p	$\hat{\phi}_{(2-3, 4, \dots, \geq 16)}$	1896.75	34
p	$\hat{\phi}_{(2-3, 4, \dots, \geq 17)}$	1898.72	35
p	$\hat{\phi}_{(2-3, 4, \dots, \geq 18)}$	1900.62	36
p	$\hat{\phi}_{(2-3, 4, \dots, \geq 19)}$	1902.70	37
p	$\hat{\phi}_{(a)}$	1904.79	38
$P_{(a)}$	$\hat{\phi}_a$	1929.85	55

for birds aged ≥ 4 years. Comparison between this model and the corresponding model where survival was not dependent on sex (i.e. $p, \hat{\phi}_{(2-3, \geq 4)}$) also supported the hypothesis that the variable sex was not needed to describe the process that gave rise to the data. This was the model with the lowest QAICc, providing some evidence of an influence of age on survival probability. In this model, the youngest individuals had a lower survival rate ($\hat{\phi}_{2-3} = 0.52$, $\hat{\text{SE}} = 0.17$; $\hat{\phi}_{\geq 4} = 0.85$, $\hat{\text{SE}} = 0.06$); the recapture probability \hat{p} was 0.39 ($\hat{\text{SE}} = 0.03$). However, the model with constant survival ($p, \hat{\phi}$) had a QAICc value only a little higher (Table 3) and consequently can be considered as a candidate model as well. The survival probability $\hat{\phi}$ estimated using this model was 0.84 ($\hat{\text{SE}} = 0.06$; $\hat{p} = 0.39$, $\hat{\text{SE}} = 0.03$). Finally, the models in which survival varies linearly or quadratically with age [p , $\text{logit}(\hat{\phi}_a) = \alpha + \beta_1 \cdot a$; p , $\text{logit}(\hat{\phi}_a) = \alpha + \beta_1 \cdot a + \beta_2 \cdot a^2$] were not retained (Table 3). Incorporation of the quadratic term tested for a possible acceleration or deceleration of the influence of age among older individuals.

As the previous step did not provide evidence of an influence of sex on survival or recapture probability, we used data from both known- and unknown-sex individuals and performed a new analysis of the influence of age on survival probability using larger samples (Table 4). The estimated overdispersion parameter \hat{c} for the general model ($p_a, \hat{\phi}_a$, Table 4) was 1.02. The lowest-QAICc model was the same as above ($p \hat{\phi}_{(2-3, \geq 4)}$). As this model included a parameter for the youngest age-class, we built a series of models corresponding to three stages in life: very young (2–3 years), intermediate (4 – ($a - 1$)), and old ($\geq a$), with a starting at 20.

We progressively pooled very old birds with younger birds by reducing a in unit steps to 16. The estimated survival probabilities corresponding to the model with $a = 20$ were the following: ($\hat{\phi}_{2-3} = 0.54$, $\hat{SE} = 0.17$, $95\% \text{CI} = [0.24 - 0.81]$; $\hat{\phi}_{4-19} = 0.87$, $\hat{SE} = 0.05$, $95\% \text{CI} = [0.72 - 0.94]$; $\hat{\phi}_{\geq 20} = 0.63$, $\hat{SE} = 0.27$, $95\% \text{CI} = [0.15 - 0.94]$). When a was reduced to 16, the corresponding estimate of survival for the group of birds ≥ 16 years old was 0.77, with $95\% \text{CI} = [0.38 - 0.95]$. This provides limited evidence that survival may have been lower among the oldest birds, but the difference was only pronounced among those ≥ 20 years old ($< 1\%$ of our sample) and was statistically inconclusive. The overall test for an influence of age on survival provided no evidence of such an effect (Table 4). The 95% confidence interval of the estimate of slope parameter corresponding to the influence of age on survival in the linear-logistic model [p , $\text{logit}(\phi_a) = \alpha + \beta.a$] included 0 ($\hat{\beta} = -0.04$, $\hat{SE} = 0.09$, $95\% \text{CI} = [-0.22, 0.14]$). The model including a quadratic term [p , $\text{logit}(\phi_a) = \alpha + \beta_1.a + \beta_2.a^2$] was not retained either (Table 4).

Parameter estimates corresponding to the lowest-QAICc model [$p \phi_{(2-3, \geq 4)}$] are very close to the previous values ($\hat{\phi}_{2-3} = 0.54$, $\hat{SE} = 0.17$; $\hat{\phi}_{\geq 4} = 0.87$, $\hat{SE} = 0.05$; $\hat{p} = 0.38$, $\hat{SE} = 0.03$). As above, this model and the simplest model (i.e. p, ϕ) have very close QAICc values (Table 4). This indicates that the simplest model is also a reasonable candidate model. The survival estimate derived from this model ($\hat{\phi} = 0.85$, $\hat{SE} = 0.05$) is also consistent with that derived in the previous analysis using data on known-sex individuals exclusively.

4.2 Survival and movement probabilities between sites

In this set of models (Table 5), we included all birds recaptured at either site that were of known age, either of known or unknown sex ($n = 1599$). As above, we first sought a model for recapture probability. We did not find evidence of an influence of age on this parameter, but there was an unambiguous influence of site (Table 5). The models without the influence of site on p are the highest-AICc models. We then tested the hypotheses of an influence of age and site on survival probability.

TABLE 5. Influence of age and site on movement, survival and recapture probabilities

	Model ^a		AICc	NP ^b
p^r	S	ψ	2593.43	20
p^r	S	$\psi_1^{12}, \psi_{\geq 2}^{12}, \psi^{21}$	2595.46	21
p^r	S	ψ^{rs}	2597.17	22
p^r	S	ψ^{12}, ψ_a^{21}	2599.22	23
p^r	$S_1, S_{\geq 2}$	$\psi_1^{12}, \psi_2^{12}, \psi_{\geq 3}^{12}, \psi^{21}$	2600.54	24
p^r	S^r	$\psi_a^{12}, \psi_1^{21}, \psi_2^{21}, \psi_{\geq 3}^{21}$	2601.27	24
p^r	$S_1, S_2, S_{\geq 3}$	$\psi_a^{12}, \psi_1^{21}, \psi_{\geq 2}^{21}$	2602.34	25
p^r	S_a	ψ_a^{12}, ψ^{21}	2604.43	26
p^r	$\text{Logit}(S_{a+r}) = \alpha + \beta.a + \delta.r$	ψ_a^{rs}	2606.43	27
p^r	S_a^r	ψ_a	2607.03	28
$\text{Logit}(p_{a+r}) = \alpha + \beta.a + \delta.r$	S_a^r	ψ_a^{rs}	2610.13	31
p_a^r	S_a^r	ψ_a^{rs}	2616.18	32
p	S_a^r	$\text{Logit}(\psi_a) = \alpha + \beta.a$	2617.68	27
p_a	S_a^r	ψ_a^{rs}	2621.37	30

^aFor notation, see text. Age-classes (subscripts): 1 = [2-4 yr], 2 = [5-9 yr], 3 = [10-14 yr], 4 = [≥ 15 yr]. Strata (superscripts): 1 = Bird Island; 2 = Ram Island.

^bNumber of parameters.

Due to insufficient data, ψ_1^{12} was fixed to zero.

We did not find evidence of a difference in survival between sites. In addition, neither the overall test for an influence of age on S , nor the approach consisting of pooling age-classes progressively provided evidence that survival depends on age. This is consistent with the results for Bird Island only. Indeed, we could not allow the youngest individuals (2-4 year) to have their own survival parameter in the two-site models, although this was the main origin of the influence of age on S that we detected in the one-site analysis.

To continue model selection, we used models with no effect of age or site on survival. In the lowest-AICc model, ψ did not depend on age or site. We did not find evidence of an influence of age on movement probability, either by testing for the overall influence of age on movement probability, or by pooling age-classes progressively within each site. Comparisons between the latter set of models and the model without an influence of age on ψ should be more powerful as the overall test for the influence of age on this parameter. Estimates made under the lowest-AICc model ($p^r S \psi$) show that survival probability is higher than the values we obtained using data from Bird Island only. The estimated survival probability for both sites combined is 0.91 ($\hat{SE} = 0.05$), the estimated probability of movement between sites is 0.08 ($\hat{SE} = 0.02$), and the estimated recapture probabilities are 0.39 ($\hat{SE} = 0.03$) at Bird Island and 0.15 ($\hat{SE} = 0.03$) at Ram Island. The model with the second-lowest AICc value has movement probabilities depending on site, but not on age. Parameter estimates corresponding to the latter model are as follows: $\hat{p}^1 = 0.39$ ($\hat{SE} = 0.03$), $\hat{p}^2 = 0.15$ ($\hat{SE} = 0.03$), $\hat{S} = 0.91$ ($\hat{SE} = 0.05$), $\hat{\psi}^{12} = 0.08$ ($\hat{SE} = 0.03$), $\hat{\psi}^{21} = 0.07$ ($\hat{SE} = 0.05$).

Finally, because the previous analyses had shown no influence of age on any parameter, we pooled all birds of known and unknown age ($n = 2367$) and re-ran model ($p^r S \psi^{rs}$). The parameter estimates were: $\hat{p}^1 = 0.42$ ($\hat{SE} = 0.03$), $\hat{p}^2 = 0.17$ ($\hat{SE} = 0.02$), $\hat{S} = 0.88$ ($\hat{SE} = 0.04$), $\hat{\psi}^{12} = 0.08$ ($\hat{SE} = 0.02$), $\hat{\psi}^{21} = 0.04$ ($\hat{SE} = 0.01$).

4.3 Emigration to other sites

4.3.1 Great Gull Island. Five birds trapped at Ram Island and two trapped at Bird Island in 1995 or 1996 were retrapped at Great Gull Island in 1996 or 1997. All these birds had originally been banded at Great Gull Island between 1987 and 1993 (three as adults and four as chicks). These birds represented 0.6% of the banded birds trapped at Ram Island in 1995 or 1996 and $< 0.2\%$ of those trapped at Bird Island. We did not attempt formal modelling of movement probabilities, however, because information on the proportion of birds trapped at Great Gull Island in 1996 and 1997 was not supplied.

4.3.2 Plymouth Beach. The 1034 birds trapped at Plymouth Beach in 1994 did not include any of the 857 birds trapped at Bird Island in 1991 or the 850 birds trapped there in 1992. Assuming for purposes of calculation that 1% of the surviving birds from Bird Island had moved to Plymouth Beach in each year, and that the annual survival rate was 0.90, the expected total number of these birds present at Plymouth Beach in 1994 would have been 32.5, and the expected number trapped would have been 4.3. Hence, it is likely that the movement probability from Bird Island to Plymouth Beach in those years was substantially lower than 0.01 year^{-1} .

5 Discussion

5.1 Modelling issues

The main difficulty we encountered arose from the large number of states (26 age-classes \times 3 'sexes' \times 2 locations) and the fact that many of the cells in the data matrices were empty, so that we could not build models accounting for all sources of variation without starting with some simplifying assumption concerning the influence of age on survival (e.g. survival varying linearly or quadratically with age). Although the latter hypotheses were reasonable (and we addressed them) it was desirable to start with more general models that did not rely on any parametric assumption about the form of the effect of age among age-classes (i.e. age as a factor). Consequently, we started with the most general models and ran several sets of models, reduced in different ways. We pooled all known-sex birds aged 16-25 in 1995 into one age-class (or all birds aged 20-25 years when sex was not taken into account) and all birds aged 2-3 years into another, so that we were unable to test for possible age-related changes within these classes. Also, we tested for influences of sex only within the subset of data for Bird Island; finding no effects of sex within this subset, we pooled birds of all three sexes for all subsequent analyses, including all analyses involving data from both islands. The consequence of this procedure is that we could not test formally for an interaction between site and sex in determining survival; nor could we test for an influence of sex on movement probabilities. Although it is biologically implausible that sex would influence survival at one site but not the other, it would have been desirable to test whether dispersal between the sites might have been sex-specific. However, the small number of birds that were detected moving between sites and the small number of birds sexed at Ram Island in 1995 made it impossible to test the latter hypothesis, as well as limiting the power of our study to detect an effect of age on movement probabilities.

5.2 Study design

The power of our study design to detect influences of age on survival rate, recapture rates, or movement rates between the two islands was relatively low. For example, the 95% confidence limits on the survival rate of the birds aged 16-25 years at Bird Island were 0.38 and 0.95; these limits were even wider (0.15-0.94) for the subset of birds aged 20-25 years. Generally, the relationship between QAICc values and the number of parameters (Tables 3 and 4) shows that variation in QAICc is largely explained by the number of parameters in the model. This is probably because of the low recapture rates (0.42 at Bird Island and 0.17 at Ram Island) in 1996, combined with the small numbers of birds in the oldest age-classes (Table 1). The low recapture rate was a practical limitation imposed by the large number of birds breeding at each site; including unbanded birds, this study required more than 2300 captures in 1996 even to achieve these low recapture rates. Most previous studies of age-specific survival in seabirds have been conducted in smaller breeding colonies (i.e. with smaller numbers of individuals), but many have achieved higher re-encounter rates and all have continued for multiple years (e.g. Buckland, 1982; Bradley *et al.*, 1989; Aebischer & Coulson, 1990; Harris *et al.*, 1994; Cam & Monnat, 2000; Sagar *et al.*, 2000). However, many of the previous studies have also reported wide confidence limits on estimated survival rates, especially for the older age-classes (e.g. Bradley *et al.*, 1989; Harris *et al.*, 1994),

so that declines in survival with increasing age can only be detected if they are very marked. This may be an unavoidable feature of studies conducted using rigorous mark-recapture techniques, unless larger samples can be obtained for the older age-classes, and/or unless recapture rates approach 1.0. Achieving high recapture rates usually requires a small study population (hundreds of individuals in the breeding colony rather than thousands; e.g. Cam & Monnat, 2000). Recapture rates also depend on marking techniques: durable colour-bands (Pugesek *et al.*, 1995) or implanted transponders (Becker & Wendeln, 1997) allow efficient re-encounters without the need for intensive searching or trapping. Small study populations require that studies be continued for many years in order to achieve adequate precision, especially for the older age-classes. Thus, designing studies of age-specific survival involves complex trade-offs between sample sizes, marking techniques, study durations and precision (Nisbet, 2001).

Most of the studies of seabirds cited in the previous paragraph reported significant declines in survival among the older-age-classes (Buckland, 1982, is an exception). Our failure to detect such a decline is not necessarily inconsistent with these positive findings, for several reasons. First, our estimates of survival have wide confidence intervals, especially for older groups. Secondly, our study was limited to one year's survival (three years' recaptures), whereas all the other studies covered multiple years, with the possibility of confounding effects of age and time if overall survival rates changed with time. Only a few of the studies controlled rigorously for this possible confounding by modelling effects of age and year simultaneously. Thirdly, any decline in survival among the oldest age-classes could have been offset by selective survival of high-quality birds (see Section 5.4). This is a feature common to the vast majority of studies of wild animal population based on resighting or recapture data (but see McDonald *et al.*, 1996, for an attempt to account for individual heterogeneity in survival).

5.3 Biological findings

A number of mark-recapture studies have used multistate models to investigate survival and movement among multiple sites (e.g. Hestbeck *et al.*, 1991; Brownie *et al.*, 1993; Spendelov *et al.*, 1995). Our study is unusual in that it coincided with a colonizing event. The common tern colony at Ram Island was founded in 1992 and increased very rapidly during the period 1993-1996, in large part by immigration from Bird and Great Gull Islands (see Section 2.2). This immigration included both first-time breeders and birds that had previously bred. Hence, it was not surprising that 8% of the birds that bred at Bird Island in 1995 moved to Ram Island in 1996. It was more noteworthy that 4-8% of the birds that bred at Ram Island in 1995 moved back to Bird Island in 1996. This return movement occurred despite the fact that Ram Island was much less crowded in both years, and that breeding success at Ram Island had been much higher in 1995 (Nisbet, unpublished data). In addition, some birds that bred at Ram Island in 1995 or 1996 moved to Great Gull Island in 1996 or 1997 (at least 0.3% emigration per year). It is noteworthy that all the birds that moved from Ram Island to Great Gull Island (5/5) had been originally marked at Great Gull Island, whereas almost all the marked birds that moved from Ram Island to Bird Island (8/9) had been originally marked at Bird Island. These findings indicate that some of the birds that settled in the new and expanding colony at Ram Island did so only temporarily, and that those

that left returned to their original breeding site. This is consistent with results obtained by Prévot-Julliard (1996) for the black-headed gull (*Larus ridibundus*).

Our best estimates of annual adult survival rate for Ram and Bird Islands combined are 0.91 ± 0.05 from birds that were of known age in 1995 ($n = 1599$), and 0.88 ± 0.04 from all birds in the study ($n = 2367$). The difference between these two estimates, although not statistically significant, suggests that there may have been some heterogeneity in the latter group, but we did not detect any other differences through formal modelling. Our two estimates of annual survival rate are consistent with three previously published estimates for the species, all of which were in the range 0.89–0.925 (Nisbet, 1978; DiCostanzo, 1980; Wendeln & Becker, 1998). None of these estimates, however, was based on formal mark-recapture modelling incorporating estimates of recapture rate, and the last two were of local survival only and may have been lower than true survival rates.

Our results provide some evidence of lower survival rates among birds 2–3 years old, i.e. first-time breeders (Tables 3 and 4). We were unable to confirm this result in our two-site analysis (Table 5), but in that analysis we could not separate birds aged 2–3 from birds aged 4. Similar differences have been reported in several previous studies of seabirds (Rattiste & Lilleleht, 1987; Bradley *et al.*, 1989; Aebischer & Coulson, 1990; Harris *et al.*, 1994). Our study was not designed to sample first-time breeders systematically (see the Methods section), but any bias would have been towards early breeders, i.e. putatively higher-quality individuals.

Our best estimates of recapture rates derived from the models were 0.42 ± 0.02 at Bird Island and 0.17 ± 0.01 at Ram Island. These are estimates of the proportion of banded birds in the study cohort known to be alive and present at each site in 1996 that were trapped in 1996. They can be compared with the known recapture rates of all birds attending nests on the islands in 1996 that were trapped in 1996; these rates are 0.45 and 0.18, respectively (see the Methods section). The modelled rates were slightly smaller, but not significantly so. This suggests that the proportion of birds that were alive in 1996 but did not attend nests was low, probably in the range 0–7%. This proportion would have included both birds that did not breed in 1996 and any birds that bred late in the season. This comparison places a low upper limit on the proportion of non-breeders at the study sites in 1996.

5.4 Within-generation mortality selection

There is growing awareness that within-generation phenotypic mortality selection (Endler, 1986) is likely to mask senescence (e.g. Vaupel & Yashin, 1985a,b; McDonald *et al.*, 1996; Nichols *et al.*, 1997; Service, 2000; Cooch *et al.*, this issue). In other words, when heterogeneity in survival rates among individuals is not taken into account, one may erroneously conclude from studies at the population level that the hypothesis of senescent decline in survival is rejected (Vaupel & Yashin, 1985a). In some circumstances, this confounding can theoretically lead to the opposite error (i.e. a decline is detected at the population level, when this pattern does not reflect change at the individual level; Vaupel & Yashin, 1985b). In addition, mortality selection may also contribute to apparent increases in survival in younger age-classes (e.g. Curio, 1983).

One way to address the question of heterogeneity in survival rates among individuals and its effect on the perceived influence of age on survival at the population level is to use a criterion to classify individuals into groups, assuming that the criterion specified *a priori* leads to definition of groups with homogeneous

risk of death. Such criteria may be defined using assumptions about the relationship between individual quality and life-history traits, e.g. age of recruitment (McDonald *et al.*, 1996), or breeding state (Cam & Monnat, 2000). However, little is known about the relevance of these *a priori* criteria, because of the absence of modelling tools required to address the relationship between these criteria and the degree of heterogeneity in the corresponding groups in situations where the recapture/resighting probability is less than one. In addition, in this type of situation, assessment of age of recruitment also requires approaches explicitly incorporating recapture probability (e.g. Cooch *et al.*, 1999; Pradel & Lebreton, 1999). This highlights the need for development of statistical inference methods incorporating heterogeneity in survival probability among individuals, which could be used in situations where the recapture/resighting probability is less than one (see Burnham & Rexstad, 1993; Pledger & Schwarz, this issue, for recovery models with these features). Development of such tools should permit assessment of the occurrence and the importance of both mortality selection and senescence in wild animal populations. This should provide a means for forming a pool of robust empirical results needed for evolutionary studies of senescence.

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REFERENCES

- AEBISCHER, N. J. & COULSON, J. C. (1990) Survival of the kittiwake in relation to sex, year, breeding experience and position in the colony, *Journal of Animal Ecology*, 59, pp. 1063-1071.
- ANDERSON, D. R. & BURNHAM, K. P. (1999) Understanding information criteria for selection among capture-recapture or ring recovery models, *Bird Study*, 46 (Supplement), pp. S14-S21.
- BECKER, P. H. & WENDELN, H. (1996) Ring removal in terns caught in Africa—a major problem for population studies, *Ringing and Migration*, 17, pp. 31-32.
- BECKER, P. H. & WENDELN, H. (1997) A new application for transponders in population ecology of the common tern, *Condor*, 99, pp. 534-538.
- BLARER, A., DOEBELI, M. & STEARNS, S. C. (1995) Diagnosing senescence: inferring evolutionary causes from phenotypic patterns can be misleading, *Proceedings of the Royal Society of London B*, 262, pp. 305-312.
- BRADLEY, J. S., WOOLLER, R. D., SKIRA, I. J. & SERVENTY, D. L. (1989) Age-dependent survival of short-tailed shearwaters *Puffinus tenuirostris*, *Journal of Animal Ecology*, 58, pp. 175-188.
- BROWNIE, C., HINES, J. E., NICHOLS, J. D., POLLOCK, K. H. & HESTBECK, J. B. (1993) Capture-recapture studies for multiple strata including non-Markovian transitions, *Biometrics*, 49, pp. 1173-1187.
- BUCKLAND, S.T. (1982) A mark-recapture survival analysis, *Journal of Animal Ecology*, 51, pp. 831-847.
- BURNHAM, K. P. & ANDERSON, D. R. (1998) *Model Selection and Inference. A Practical Information-Theoretic Approach* (New York, Springer-Verlag).

- BURNHAM, K. P. & REXSTAD, E. A. (1993) Modeling heterogeneity in survival rates of banded waterfowl, *Biometrics*, 49, 1194-1208.
- CAM, E. & MONNAT, J.-Y. (2000) Stratification based on reproductive state reveals contrasting patterns of age-related variation in demographic parameters in the kittiwake, *Oikos*, 90, 560-574.
- CAREY, J. R., LIEDO, P., OROZCO, D. & VAUPEL, J.W. (1992) Slowing of mortality rates at older ages in large medfly cohorts, *Science*, 258, pp. 457-461.
- CHARLESWORTH, B. (1994) *Evolution in Age-structured Populations* (Cambridge, Cambridge University Press).
- CLOBERT, J. (1995) Capture-recapture and evolutionary ecology: a difficult wedding?, *Journal of Applied Statistics*, 22, 989-1008.
- COOCH, E. G., LANK, R. F., ROCKWELL, R. F. & COOKE, F. (1999) Body size and age of recruitment in snow geese *Anser c. caerulescens*, *Bird Study*, 46, 112-119.
- COULTER, M. (1986) Assortative mating and sexual dimorphism in the common tern, *Wilson Bulletin*, 98, pp. 93-100.
- DANN, P. & CULLEN, J. M. (1990) Survival, patterns of reproduction, and lifetime reproductive output in little blue penguins (*Eudyptula minor*) on Phillip Island, Victoria, Australia. In: L. S. DAVIS & J. T. DARBY (Eds) *Penguin Biology*, pp. 76-84 (London, Academic Press).
- DiCOSTANZO, J. (1980) Population dynamics of a common tern colony, *Journal of Field Ornithology*, 51, pp. 229-243.
- ENDLER, J. A. (1986) *Natural Selection in the Wild* (Princeton, Princeton University Press).
- FINCH, C. E. (1990) *Longevity, Senescence, and the Genome* (Chicago, University of Chicago Press).
- FORSLUND, P. & PÄRT, T. (1995) Age and reproduction in birds—hypotheses and tests, *Trends in Ecology and Evolution*, 10, pp. 374-378.
- GAILLARD, J.-M., ALLAINE, D., PONTIER, D., YOCOZO, N. & PROMISLOW, D. L. (1994) Senescence in natural populations of mammals: a reanalysis, *Evolution*, 48, pp. 509-516.
- GALBRAITH, H., HATCH, J. J., NISBET, I. C. T. & KUNZ, T. H. (1999) Age-specific reproductive efficiency in common terns *Sterna hirundo*: measurement of energetic expenditure using doubly-labelled water, *Journal of Avian Biology*, 30, pp. 85-96.
- HARLOW, R. A., Jr. (1995) Ram Island: recovery in progress, *Bird Observer*, 23, pp. 333-338.
- HARRIS, M. P., BUCKLAND, S. T., RUSSELL, S. M. & WANLESS, S. (1994) Year- and age-related variation in the survival of adult European shags over a 24-year period, *Condor*, 96, pp. 600-605.
- HAYS, H., LIMA, P., MONTEIRO, L., DiCOSTANZO, J., CORMONS, G., NISBET, I. C. T., SALIVA, J., SPENDELOW, J. A., BURGER, J., PIERCE, J. & GOCHFELD, M. (1999) A wintering concentration of roseate and common terns in Bahia, Brazil, *Journal of Field Ornithology*, 70, pp. 455-464.
- HESTBECK, J. B., NICHOLS, J. D. & MALECKI, R. A. (1991) Estimates of movement and site fidelity using mark-recapture data of wintering Canada geese, *Ecology*, 72, pp. 525-533.
- HOLMES, D. J. & AUSTAD, S. N. (1995a) Birds as animal models for the comparative biology of aging: a prospectus, *Journal of Gerontology*, 59A, pp. B59-B66.
- HOLMES, D. J. & AUSTAD, S. N. (1995b) The evolution of avian senescence patterns: implications for understanding primary aging processes, *American Zoologist*, 35, pp. 307-317.
- LEBRETON, J.-D. (1995) The future of population dynamics studies using marked individuals: a statistician's perspective, *Journal of Applied Statistics* 22, pp. 1009-1030.
- LEBRETON, J.-D., BURNHAM, K. P., CLOBERT, J. & ANDERSON, D. R. (1992) Modeling survival and testing biological hypotheses using marked animals: a unified approach with case studies, *Ecological Monographs*, 62, pp. 67-118.
- LITTELL, R. C., MILLIKEN, G. A., STROUP, W. W. & WOLFINGER, R. D. (1996) *SAS System for Mixed Models* (Cary, NC, SAS Institute).
- LOISON, A., FESTA-BIANCHET, M., GAILLARD, J.-M., JORGENSON, J. T. & JULLIEN, J.-M. (1999) Age-specific survival in five populations of ungulates: evidence of senescence, *Ecology*, 80, pp. 2539-2554.
- MCDONALD, D. B., FITZPATRICK, J. W. & WOOLFENDEN, G. E. (1996) Actuarial senescence and demographic heterogeneity in the Florida scrub jay, *Ecology*, 77, pp. 2373-2381.
- MERTZ, D. B. (1975) Senescent decline in flour beetle strains selected for early adult fitness, *Physiological Zoology*, 48, pp. 1-23.
- MILLS, J. A. (1989) Red-billed gull. In: I. NEWTON (Ed), *Lifetime Reproduction in Birds*, pp. 387-404 (London, Academic Press).
- NICHOLS, J. D. (1992) Capture-recapture models using marked animals to study population dynamics, *BioScience*, 42, pp. 94-102.
- NICHOLS, J. D. & KENDALL, W. L. (1995) The use of multi-state capture-recapture models to address questions in evolutionary ecology, *Journal of Applied Statistics*, 22, pp. 835-846.

- NICHOLS, J. D., HINES, J. E. & BLUMS, P. (1997) Tests for senescent decline in annual survival probabilities of common pochards, *Aythya ferina*, *Ecology*, 78, pp. 1009–1018.
- NISBET, I. C. T. (1973) Terns in Massachusetts: present numbers and historical changes, *Bird-Banding*, 44, pp. 27–55.
- NISBET, I. C. T. (1978) Population models for common terns in Massachusetts, *Bird-Banding*, 49, pp. 50–58.
- NISBET, I. C. T. (1996) Post-fledging survival in common terns in relation to brood order, hatching date and parental age, *Colonial Waterbirds*, 19, pp. 253–255.
- NISBET, I. C. T. (2001) Detecting and measuring senescence in wild birds: experience with long-lived seabirds, *Experimental Gerontology*, 36, pp. 833–843.
- NISBET, I. C. T. (Forthcoming) Common tern. In: A. POOLE & F. GILL (Eds), *The Birds of North America* (Philadelphia, PA, The Birds of North America, Inc).
- NISBET, I. C. T. & HATCH, J. J. (1988) Durability of incoloy bands on common terns, *Colonial Waterbirds*, 11, pp. 113–114.
- NISBET, I. C. T., WINCHELL, J. M. & HEISE, A. E. (1984) Influence of age on the breeding biology of common terns, *Colonial Waterbirds*, 7, pp. 117–126.
- NISBET, I. C. T., BURGER, J., SAFINA, C. & GOCHFELD, M. (1990) Estimating fledging success and productivity in roseate terns (*Sterna dougallii*), *Colonial Waterbirds*, 13, pp. 85–91.
- NISBET, I. C. T., APANIUS, V. & FRIAR, M. S. (Forthcoming) Breeding performance of very old common terns, *Journal of Field Ornithology*, in press.
- PARTRIDGE, L. (2001) Evolutionary theories of ageing applied to long-lived organisms, *Experimental Gerontology*, 36, pp. 641–650.
- PRADEL, R. & LEBRETON, J.-D. (1999) Comparison of different approaches to the study of local recruitment of breeders, *Bird Study*, 46 (Supplement), pp. S74–S81.
- PRÉVOT-JULLIARD, A. C. (1996) Rôle de la dispersion dans la dynamique d'une population de mouette rieuse *Larus ridibundus* L. (Montpellier, France, Thèse de l'Université de Montpellier II).
- PUGESEK, B. H., NATIONS, C., DIEM, K. L. & PRADEL, R. (1995) Mark-resighting analysis of a California gull population, *Journal of Applied Statistics*, 22, pp. 625–640.
- RATTISTE, K. & LILLELEHT, V. (1987) Population ecology of the common gull *Larus canus* in Estonia, *Ornis Fennica*, 64, pp. 25–26.
- RATTISTE, K. & LILLELEHT, V. (1995) Survival rates of breeding common gulls in Estonia, *Journal of Applied Statistics*, 22, pp. 1057–1062.
- RICKLEFS, R. E. (1998) Evolutionary theories of aging: confirmation of a fundamental prediction, with implications for the genetic basis and evolution of life span, *American Naturalist*, 147, pp. 1047–1071.
- RICKLEFS, R. E. (2000) Intrinsic aging-related mortality in birds, *Journal of Avian Biology*, 31, pp. 103–111.
- SERVICE, P.M. (2000) Heterogeneity in individual mortality risk and its importance for evolutionary studies of senescence, *American Naturalist*, 156, pp. 1–13.
- SOMMERS, L. A. & ALFIERI, M. A. (1998) *1997 Long Island Colonial Waterbird and Piping Plover Survey* (Stony Brook, NY, New York State Department of Environmental Conservation).
- SPENDELOW, J. A., NICHOLS, J. D., NISBET, I. C. T., HAYS, H., CORMONS, G. D., BURGER, J., SAFINA, C., HINES, J. E. & GOCHFELD, M. (1995) Estimating annual survival and movement rates of adults within a metapopulation of roseate terns, *Ecology*, 76, pp. 2415–2428.
- TATAR, M., CAREY, J. R. & VAUPEL, J. W. (1993) Long-term cost of reproduction with and without accelerated senescence in *Callosobruchus maculatus*: analysis of age-specific mortality, *Evolution*, 47, pp. 1302–1312.
- VAUPEL, J. W. & YASHIN, A. I. (1985a) Heterogeneity's ruses: some surprising effects of selection on population dynamics, *American Statistician*, 39, pp. 176–185.
- VAUPEL, J. W. & YASHIN, A. I. (1985b) The deviant dynamics of death in heterogeneous populations. In: B. N. TUMA (Ed), *Sociological Methodology*, pp. 180–211 (San Francisco, CA, Jossey-Bass).
- VIALLEFONT, A., COOKE, F. & LEBRETON, J.-D. (1995) Age-specific costs of first-time breeding. *Auk*, 112, pp. 67–76.
- WEIMERSKIRCH, H. (1992) Reproductive effort in long-lived birds: age-specific patterns of condition, reproduction, and survival in the wandering albatross, *Oikos*, 64, pp. 464–473.
- WENDELN, H. & BECKER, P. H. (1996) Body mass changes in breeding common terns *Sterna hirundo*, *Bird Study*, 43, pp. 85–95.
- WHITE, G. C. & BURNHAM, K. P. (1999) Program MARK—survival estimation from populations of marked animals, *Bird Study*, 46 (Supplement), pp. S120–S139.